

Anatomical Studies of *Sphaeropteris* and *Cnemidaria* (Cyatheaceae)¹

TERRY W. LUCANSKY

Department of Botany, University of Florida, Gainesville, FL 32611

Despite a renewal of interest in the tree ferns (Tryon, 1970, Gastony, 1973, 1974, 1981; Gastony & Tryon, 1976; Stolze, 1974), relatively little is known anatomically about these largest of ferns. Previous anatomical studies have dealt primarily with mature paleotropical species (Bower, 1912; Ogura, 1927, 1972; Godwin, 1932; Mehra & Singh, 1955) and have shown that similarities between genera occur in both the vascular anatomy and nodal patterns. Recent studies of mature members of the neotropical Cyatheaceae also have shown striking similarities among the genera (Lucansky, 1974b, 1976b, 1977; Lucansky & White, 1974).

Tryon (1970) revised the classification of the family Cyatheaceae and recognized six genera and three principal evolutionary lines among the squamate genera. *Sphaeropteris* with its undifferentiated (conform) scales represents an evolutionary line and occurs at the base of the squamate genera, while *Cnemidaria* with its marginate scales is found at the top of another evolutionary line. *Sphaeropteris* supposedly contains elements allied to the other two major evolutionary groups in the family (Tryon & Tryon, 1982). On the basis of scale characters, *Sphaeropteris* subgenus *Sphaeropteris* is related to *Alsophila* and subgenus *Sclephropteris* is allied with *Trichipteris*, *Cyathea* and *Cnemidaria*. Holttum and Edwards (1983) believe that this latter alliance (together with certain species of Tryon's *Sphaeropteris*) forms a natural group which needs a new subdivision.

Holttum (1963, 1964, 1965) also has intensively studied the Cyatheaceae, but recognized only a single genus *Cyathea* for the same taxa in the family. He subdivided the genus on the basis of characters of the stipe scales and associated characters of indusia, hairs and venation, and felt that the only sharp subdivision within the genus is between the subgenus *Sphaeropteris* and the subgenus *Cyathea* (Holttum, 1982; Holttum & Edwards, 1983). His subgenus *Sphaeropteris* is characterized by peculiar marginal setae on the stipe scales and certain indusial and venation characters, while Tryon (1970) regarded the uniformity of cells of the stipe scales as the most important character for delimiting the genus *Sphaeropteris*. Although Tryon (1970) promoted subgenus *Sphaeropteris* to generic rank, Holttum & Edwards (1983) feel that it is not a natural group and contains species that do not belong in the group.

Sphaeropteris sensu Tryon is a genus of approximately 120 species found in both the New and Old World. Its distinctive feature is the presence of conform stipe scales with undifferentiated or poorly differentiated cellular construction

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(Tryon, 1970). In some respects (e.g. leaf morphology, position of trichomes and indusium) this genus is similar to the other squamate genera in the Cyatheaceae.

Cnemidaria sensu Tryon, is a genus of 25 species confined to the American tropics. Its closest relationship is with *Cyathea* (Tryon & Tryon, 1982), and Holttum even includes it in subgenus *Cyathea* of the genus *Cyathea* (Holttum & Edwards, 1983). According to Tryon (1970) this genus constitutes a strong evolutionary line, and several characters, including the lack (rarely present) of trichomes on the adaxial side of the costae, contrast markedly with the other squamate genera. Based upon spore morphology, venation, leaf architecture, habit and lack of trichomes adaxially on the costae, *Cnemidaria* forms the most natural and distinctive genus in the Cyatheaceae (Stolze, 1974). Holttum & Sen (1961) reinforced the distinctiveness of the genus by pointing out the peculiar character of the spores. It also is the most advanced genus in the family with its complex venation and reduced laminar architecture being end products of its adaptive development. The principal characters of *Cnemidaria* rarely, if ever, occur in the other squamate genera.

The present study is part of a broad investigation of the neotropical Cyatheaceae (Tryon, 1970; Tryon & Tryon, 1982). The anatomy of representative species of *Sphaeropteris* and *Cnemidaria* is elucidated to provide data that can be used to determine the taxonomic status and phyletic position of these two genera. Previous workers (Holttum & Sen, 1961; Sen, 1964; Lucansky & White, 1974) have already shown the importance of anatomy and morphology to the study of this group of plants.

MATERIALS AND METHODS

The following species were examined in this study: *Sphaeropteris elongata* (Hook.) Tryon, *S. senilis* (Kl.) Tryon, *Cnemidaria mutica* var. *mutica* (Maxon) Stolze and *C. mutica* var. *grandis* (Maxon) Stolze. Previous workers had considered these varieties of *C. mutica* to be distinct species (Maxon, 1912; Christensen, 1938; Tryon, 1970). Developing shoot tips were collected along roadsides or in montane and lowland rainforests in Costa Rica and Venezuela. Voucher specimens are on file in the herbarium of Duke University (DUKE).

Plant materials were killed and fixed in formalin-acetic acid-alcohol (FAA) and sectioned on a macrotome (Lucansky, 1976a). Sections (slices) were partitioned into manageable sizes, dehydrated in a tertiary-butyl alcohol series and embedded in paraffin (Johansen, 1940). Sections (8 μ m) were made and stained with safranin-fast green. Stained sections were photographed with a 35 mm Nikon M35 S camera, and entire slices were photographed with a 35 mm single-lens reflex camera. Unless otherwise noted, the results given are based upon the combined data of all species.

RESULTS AND DISCUSSION

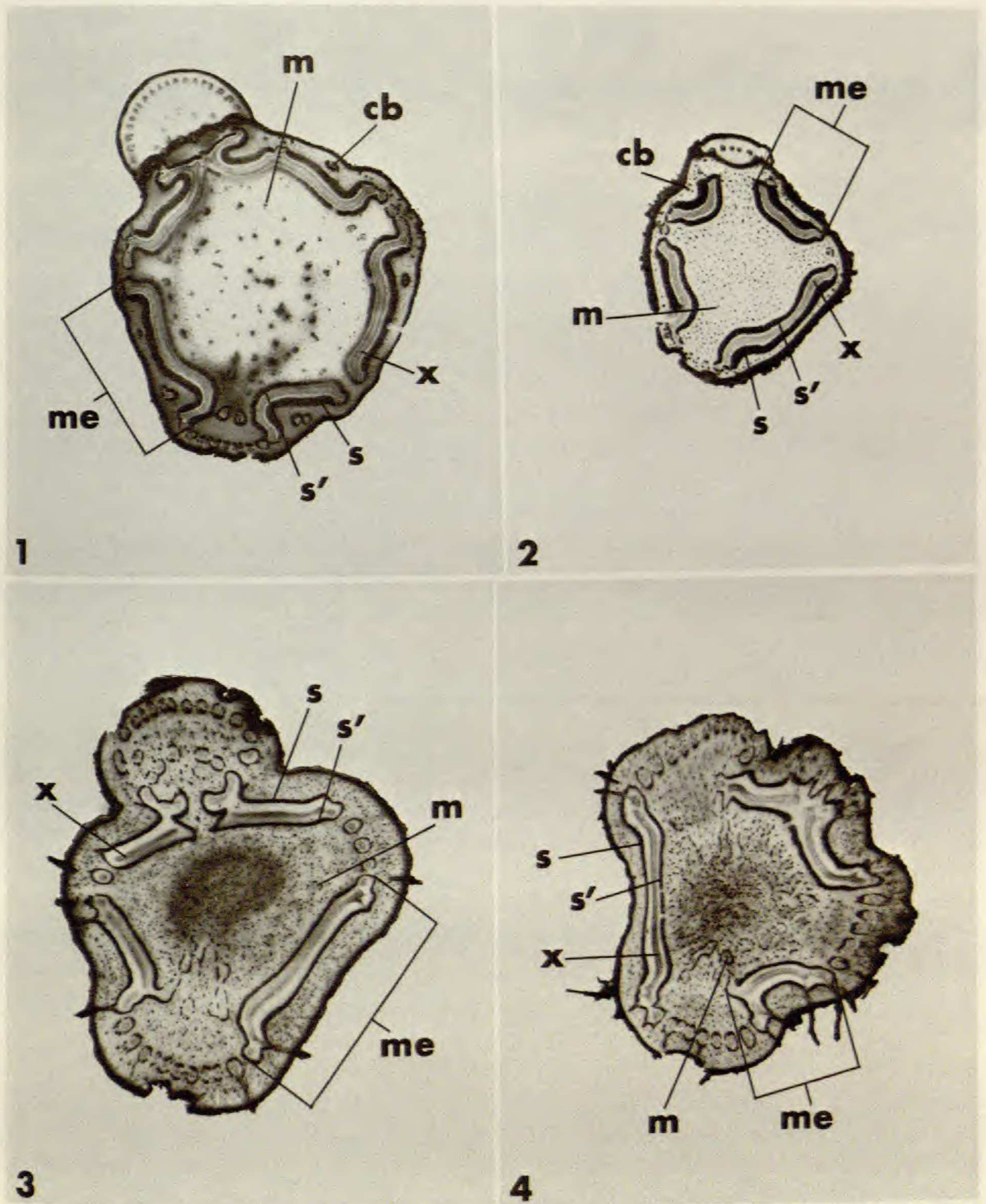
Although members of *Sphaeropteris* are arborescent, species of *Cnemidaria* are characterized by an acaulescent habit. The caudices of some species of

Cnemidaria, however, many reach 1.5 meter in length (Stolze, 1974). The stipe scales of *Sphaeropteris* are conform, whereas the scales of *Cnemidaria* are marginate. Certain species of *Sphaeropteris* may possess one or more dark apical setae on a scale, while the scales of *Cnemidaria* lack apical setae (Tryon, 1970, Tryon & Tryon 1982). The costae of *Sphaeropteris* (and other squamate genera) are pubescent adaxially, whereas trichomes, if present, occur only on the abaxial surface of the costae (and other axes) of *Cnemidaria*. A simple leaf architecture, costal areoles and a whitish arachnoid scurf also characterize *Cnemidaria*, but are lacking in *Sphaeropteris*. Spores of *Cnemidaria* with their three large equatorial pores are unique in the family Cyatheaceae (Stolze, 1974).

The stelar pattern in the mature stems of both *Sphaeropteris* and *Cnemidaria* is a dictyostele with overlapping leaf gaps and consists of individual vascular bundles (meristeles), each surrounded by sclerenchymatous tissue (Figs. 1-4). The number of meristeles varies from 3-5, depending upon the species and length of the leaf gaps.

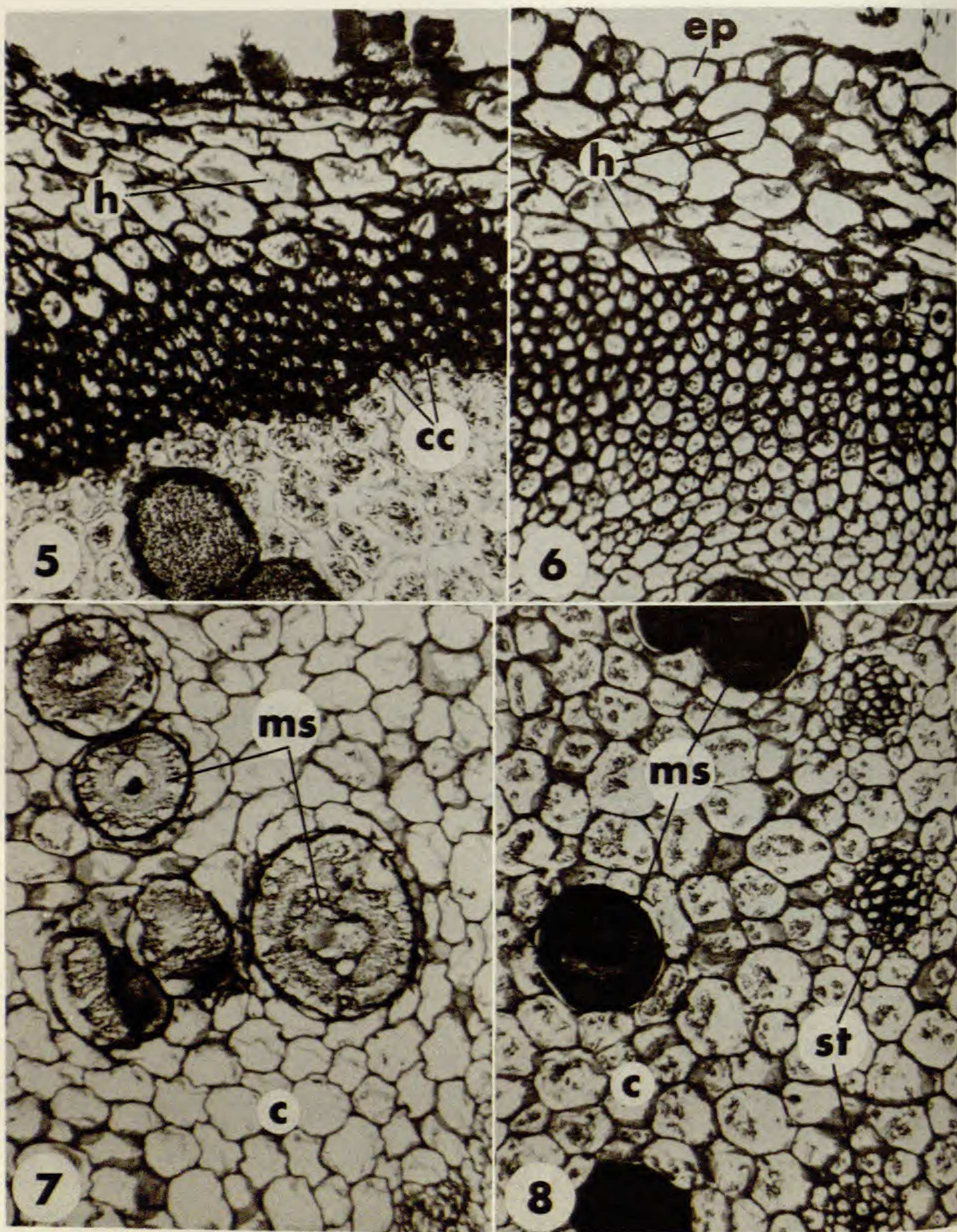
A single-layered epidermis composed of variously shaped, thick-walled cells typically is sloughed in mature sporophytes, although remnants of this layer may persist. In *S. elongata* the epidermal cells are thin-walled and occasionally filled with tannins. Previous workers had reported that the outer walls of the epidermal cells may be thickened or cutinized (Sen & Mitra, 1966; Sen, 1968). The outermost layer of the stems of both genera studied is typically a hypodermis composed of two zones that are variable in thickness (Figs. 5, 6). The outer zone typically is partially sloughed and composed of variously shaped, thick-walled parenchyma cells filled with tannins and/or starch grains. The inner zone consists of sclerified, thick-walled parenchyma cells that closely resemble fibers (Fig. 5, 6). These cells are formed by secondary sclerosis of the walls with retention of the nucleus (Sen, 1968), and generally possess tannins and/or starch grains. The inner zone in *S. elongata* may be quite extensive and possess large, randomly-distributed mucilage-sac cells—singly or in group of 2-7 cells (Fig. 10). Distinctive cubical cells (to be discussed later) are noted between the hypodermis and the cortex in both species of *Cnemidaria* and *S. senilis* (Figs. 5). In *S. senilis* the hypodermis consists of only a single zone of sclerified parenchyma cells filled with tannins. Previous workers (Ogura, 1972; Mehra & Singh, 1955) also reported a single hypodermal zone of fibers, but such a homogenous layer may be due to the loss of the outer zone of parenchyma cells or the age (young) of the plant. A two-zoned hypodermis represents a unifying character in the group, and has been previously reported for the other genera (except *Metaxya*) in the family (Lucansky, 1976b, 1977, 1982).

Although Sen (1964) found that a band of sclerenchyma tissue may occur between the cortical layers in *Dicksonia* and *Gulcita*, the cortex in the species in this study consists solely of large, thin-walled parenchyma cells filled with tannins and/or starch grains. Large mucilage-sac cells are randomly distributed in the cortex, singly or in a group of 2-10, and form an articulated laticiferlike system (Figs. 7, 8). Similar idioblasts have been reported for *Lophosoria* (Lucansky, 1982), the other squamate genera (Lucansky, 1976b, 1977) and *Dicksonia* (Williams, 1925). Schütze (1906) called these idioblasts excretion containers, rath-



FIGS. 1-4. Transsections of tree-fern stems. FIG. 1. *Sphaeropteris elongata*, $\times 8$. FIG. 2. *Sphaeropteris senilis*, $\times 1.5$. FIG. 3. *Cnemidaria mutica* var. *mutica*, $\times 1.7$. FIG. 4. *Cnemidaria mutica* var. *grandis*, $\times 1.3$. cb = cortical bundle, m = medullary bundle, me = meristele, s = external stelar sheath, s' = internal stelar sheath, x = primary xylem.

er than secretion cells, and reported that they contain fatty acids or tannins, whereas Ogura (1972) found that they contain slime. Numerous small localized areas of sclerified parenchyma cells, filled with tannins, occur within the cortex of both species of *Cnemidaria* and *S. senilis* (Fig. 8), but are lacking in *S. elon-*

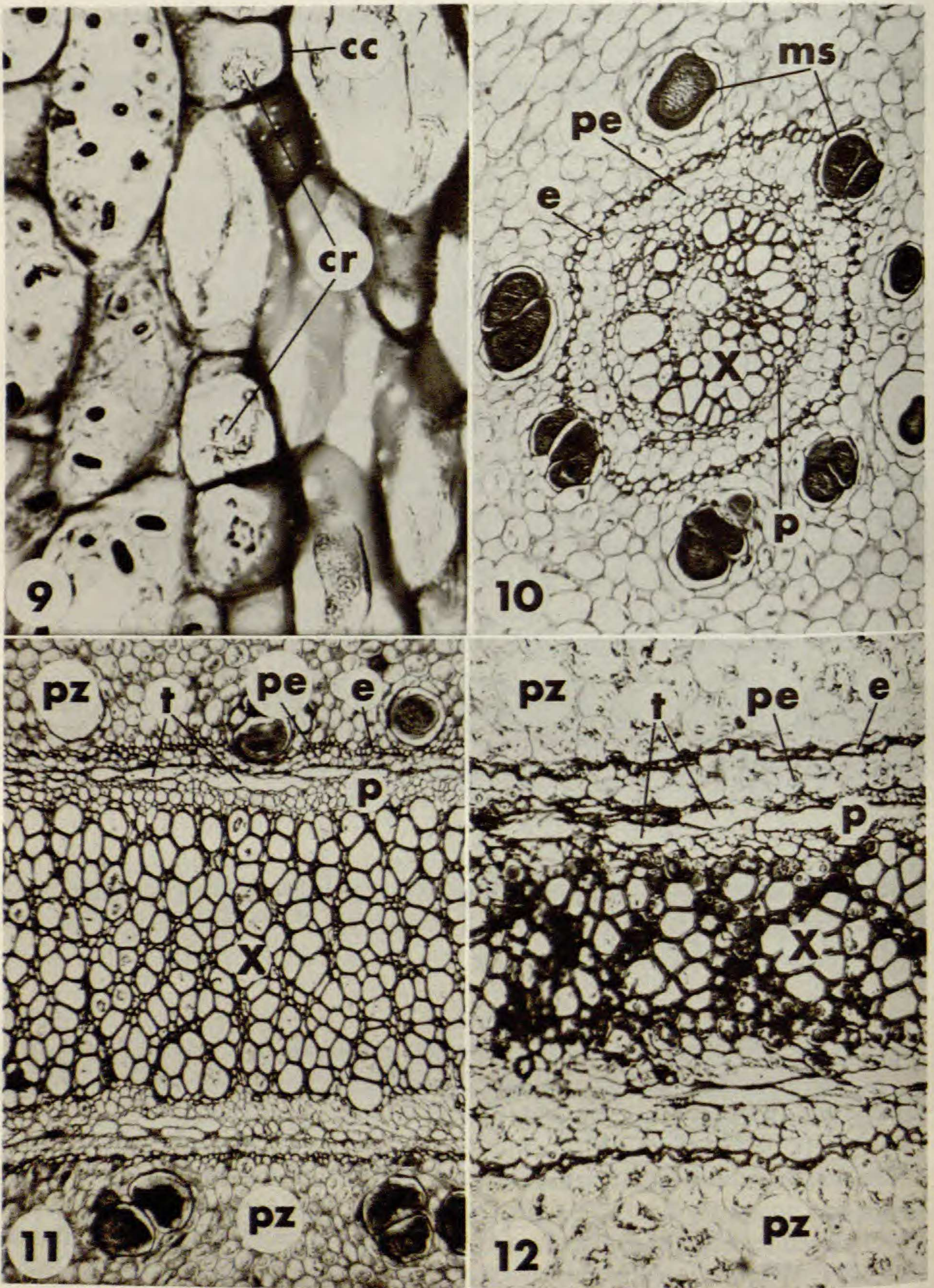


FIGS. 5-8. Anatomical details of tree-fern stems. FIG. 5. Two-zoned hypodermis of *Cnemidaria mutica* var. *grandis*, $\times 124$. Note cubical cells. FIG. 6. Two-zoned hypodermis of *Sphaeropteris elongata*, $\times 130$. FIG. 7. Mucilage-sac cells in cortical zone of *S. senilis*, $\times 126$. FIG. 8. Localized areas of sclerified parenchyma in cortex of *C. mutica* var. *grandis*, $\times 144$. c = cortex, cc = cubical cell, ep = epidermis, h, hypodermis, ms = mucilage-sac cell, st = sclerified (parenchyma) tissue.

gata. Cubical cells occur between these sclerified areas and the cortex in these species (Fig. 9). Similar areas of sclerenchyma tissue have been noted in the cortex of *Cystodium* (Sen & Mitra, 1966), *Lophosoria* (Lucansky, 1982) and some species of *Trichipteris* and *Cyathea* (Lucansky, 1977), but do not occur in *Alsophila* and *Nephelea* (Lucansky, 1976b).

Cortical bundles are a characteristic feature of the Cyatheaceae (Lucansky, 1974b, Ogura, 1972), and are not found in any other group of ferns. Cortical bundles undergo divisions and fusions, end blindly in the cortex, fuse with meristemes and leaf traces, or infrequently proceed directly to the petiole as a leaf trace (Lucansky 1974b). Schütze (1906) believed that they are possibly involved with the movement and deposition of starch in the stem. In the present study cortical bundles occur in *S. elongata* and in *S. senilis* (Fig. 10), but are lacking in both species of *Cnemidaria*. These bundles may be large and form a conspicuous feature in *S. elongata* (Figs. 1, 10), but are small and relatively indistinct in *S. senilis* (Fig. 2). Cortical bundles have previously been found in some species of *Nephelea*, *Alsophila*, and *Trichipteris* (Lucansky 1976b, 1977), but are lacking in *Cyathea*, *Metaxya*, and *Lophosoria* (Lucansky 1977, 1982). Both Stolze (1974) and Tryon (1970) believe that *Cnemidaria* has probably arisen from a line of *Cyathea*, and the lack of cortical bundles in both genera supports this contention. These accessory bundles in *Sphaeropteris* may possess a partial sheath of sclerified parenchyma cells, although Schütze (1906) reported that cortical bundles usually lack a sheath. They are surrounded by a distinct single-layered endodermis that may be filled with tannins and possess Casparian strips (Fig. 10). A parenchymatous pericycle (1-3 layers) encircles the primary phloem, which consists of both sieve cells and phloem parenchyma. No tangential cells are found in the phloem of the cortical bundles, as previously reported for *Nephelea*, *Alsophila*, and *Trichipteris* (Lucansky 1976b, 1977). Small bundles have only xylary element in their centers, whereas large bundles may have one or more parenchymatous areas within the xylary mass. The primary xylem consists of tracheids with scalariform wall thickenings, with xylem parenchyma filled with tannins interspersed among these xylary elements (Fig. 10). Xylem maturation is mesarch.

In all species a meristeme is surrounded by an external and internal stelar sheath composed of sclerified parenchyma (or sclerenchyma) cells filled with tannins. Both stelar sheaths arise from localized areas of sclerified cells that undergo fusion to form a continuous sheath (Lucansky & White, 1976). The presence of sclerified tissue around the individual meristemes is a characteristic feature of the Cyatheaceae, and had been previously noted in other cyatheoid genera (Lucansky 1976b, 1977, 1982; Ogura, 1972). Both stelar sheaths typically are delimited externally and internally by a single layer of cubical cells. These distinctive cells are greatly thickened on three walls (wall proximal to thin-walled parenchyma cells remains thin-walled), and each cell contains a single, large solitary crystal (Fig. 9). The crystalloid structure in each cell is insoluble in H_2SO_4 (Holtum & Sen, 1961) and is thought to be composed of silica (Sen, 1968). Cubical cells have been found in other genera of neotropical Cyatheaceae (Lucansky 1976b, 1977, 1982), and occur in the cortex of certain dicksonioid species



FIGS. 9-12. Anatomical details of tree-ferns stems. FIG. 9. Cubical cells with crystals in *Sphaeropteris senilis* between external stelar sheath and parenchymatous zone of a meristele, $\times 560$. FIG. 10. Large cortical bundle in *S. elongata*, $\times 123$. FIG. 11. Meristele of *S. elongata* showing tangential cells, $\times 57$. FIG. 12. Meristele of *Cnemidaria mutica* var. *mutica* showing tangential cells, $\times 120$. cc = cubical cell, cr = crystal, e = endodermis, ms = mucilage-sac cell, p = primary phloem, pe = pericycle, pz = parenchymatous zone, t = tangential cell, x = primary xylem.

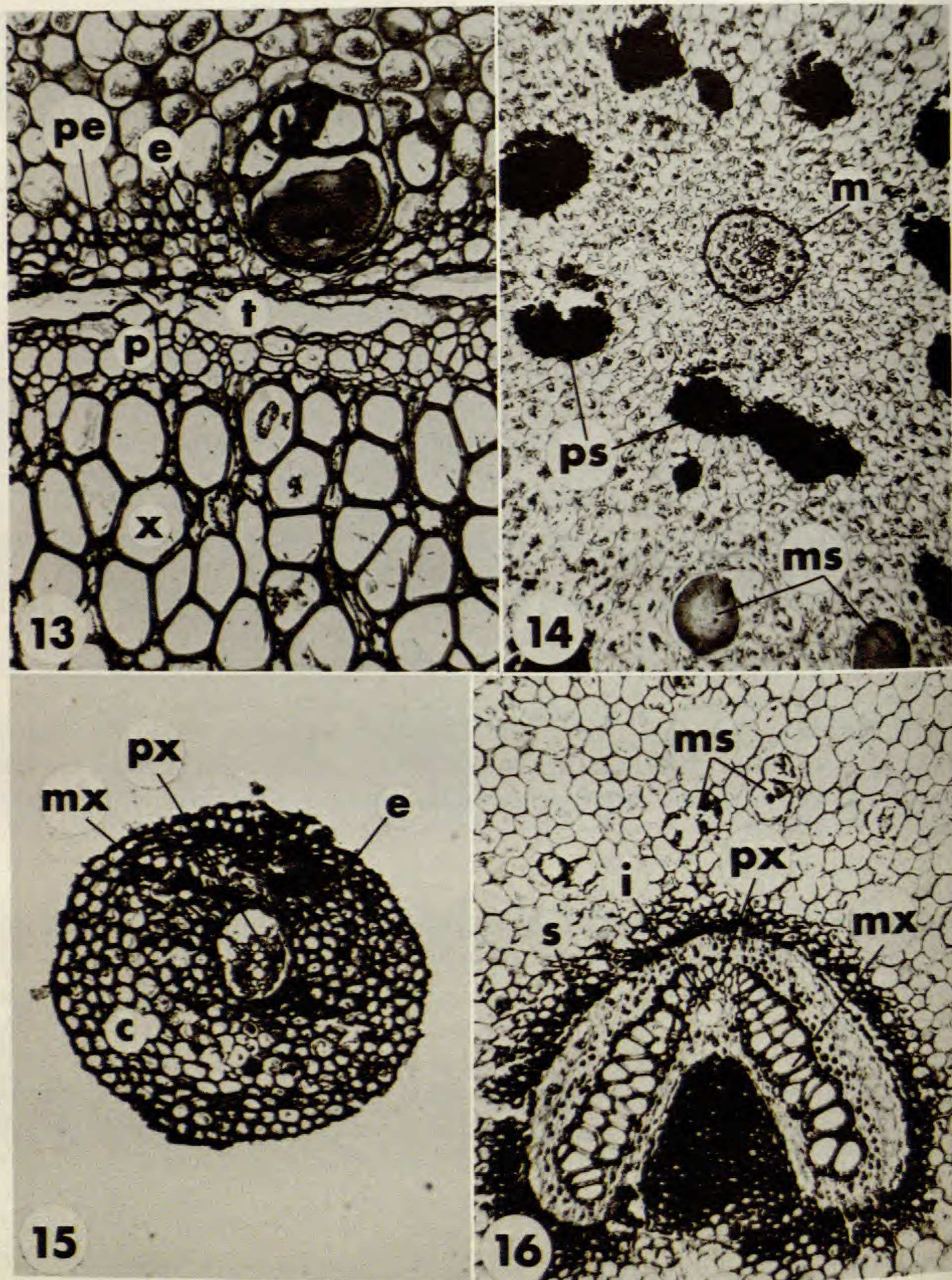
(Sen, 1964). Although Ogura (1972) thought that these cells were sclerenchyma cells, their living protoplast, wall morphology, position and resemblance to parenchyma cells in young stems indicate that they are thick-walled parenchyma. Sen (1964) also believed that they were not sclerenchyma cells based upon their rate of cell division and cellular inclusions.

A parenchymatous zone composed of large, thin-walled parenchyma cells filled with starch grains and tannins separates the stelar sheaths from each meristele (Figs. 1, 12). Large mucilage-sac cells occur singly or in groups of 2-7 within this zone (Fig. 11). Schütze (1906) believed that these parenchymatous zones may function in the conduction and storage of carbohydrates.

Each meristele in an amphicribal bundle delimited by a distinct endodermis filled with tanniferous substances (Figs. 11, 12). Distinct Casparian strips are lacking in the walls of these cells. A pericycle of 2-3 rows of thin-walled parenchyma cells completely encircles the primary phloem. Although Ogura (1927) reported that the protophloem was usually compressed, thick-walled, and swollen, the protophloem and metaphloem typically are indistinguishable in material studied. The latter tissue is composed of sieve cells, phloem parenchyma cells filled with tannins, and distinctive tangential cells (Figs. 11, 12). The phloic tangential cells are large and elongate tangentially in transection (Fig. 13) and form a characteristic feature of the Cyatheaceae. They are more numerous in *Cnemidaria* than in *Sphaeropteris*, and their position and pattern of arrangement is similar to that reported for the other cyatheoid genera (Lucansky 1976b, 1977, 1982). They represent specialized sieve cells that are devoid of nuclei, possess sieve areas on their lateral walls and accumulate callose (Sen, 1964), although they have been variously referred to as false sieve tubes (Schütze, 1906) or mucilage cells (Ogura, 1927, 1972). According to Ogura, these distinctive cells may be partially or entirely replaced by mucilage cells or longitudinally elongate cells.

The primary xylem is primarily composed of tracheids with scalariform wall thickenings, with xylem parenchyma cells filled with tannins and starch grains interspersed among these tracheary elements (Figs. 11, 12). Although earlier studies (Ogura, 1927; Sen, 1964) reported that protoxylem is usually absent in the primary xylem of mature stems, tracheids with spiral wall thickenings were infrequently seen in the present study. Each meristele is composed predominantly of metaxylem and xylem maturation is mesarch in all species studied.

The pith contains large, thin-walled parenchyma cells that frequently contain starch grains and tannins. Large mucilage-sac cells occur randomly in the pith, either singly or in groups of 2-5. In all species studied, numerous medullary bundles are scattered in the pith (Fig. 14) and represent another characteristic feature of the Cyatheaceae. They have been found in the other squamate genera in the family (Lucansky, 1974b, 1976b, 1977; Ogura, 1972), but are lacking in *Metaxya* and *Lophosoria* (Lucansky, 1974a, 1982). Adams (1977) reported that the medullary bundle system of *Cyathea fulva* consists of a central network and a peripheral one composed of three types of bundles. Medullary bundles arise *de novo* in the pith (Ogura, 1927, Lucansky, 1974b) or are separated from the leaf-gap margins (Godwin, 1932; Lucansky, 1976b). They undergo fusions and



FIGS. 13-16. Anatomical details of tree-ferns stems. FIG. 13. Tangential cells in the primary phloem of meristele of *Sphaeropteris elongata*, $\times 139$. FIG. 14. Medullary bundle with partial sheath in the pith region of *Cnemidaria mutica* var. *mutica*, $\times 581$. Note mucilage-sac cells. FIG. 15. Transsection of diarch root of *S. senilis*, $\times 67$. FIG. 16. Transsection of petiole strand of *S. senilis*, $\times 71$. Note intercellular space. c = cortex, e = endodermis, i = intercellular space, m = medullary bundle, ms = mucilage-sac cell, mx = metaxylem, p = primary phloem, pe = pericycle, ps = partial sheath, px = protoxylem, s = sheath, t = tangential cell, x = primary xylem.

divisions, end blindly in the pith, fuse with a meristele or leaf trace or proceed directly to the petiole as a leaf trace (Lucansky, 1974b; Lucansky & White, 1974; Adams, 1977). The medullary bundles are identical in cellular composition to cortical bundles. Although phloic tangential cells have been found in medullary bundles of certain species of *Alsophila* and *Nephelea* (Lucansky, 1976b), no phloic tangential cells occur in these bundles in the species studied. Small medullary bundles typically have only xylary elements in their centers, whereas larger bundles may have 1-several parenchymatous areas within the xylary mass. Each bundle may be partially or totally surrounded by a partial sheath composed of sclerified parenchyma cells (Fig. 14), although Ogura (1972) reported that medullary bundles usually lack a sheath. Only those bundles located along the internal stelar sheath normally lack such tissue in the species in this study. In addition to these sheaths, variously sized localized areas of sclerified parenchyma cells are randomly scattered in the pith of both *Sphaeropteris* and *Cnemidaria*. Cubical cells occur between these areas and the pith proper. Localized areas of sclerified tissue also occur infrequently in *Nephelea* and *Trichipteris*, but commonly occur in *Cyathea* (Lucansky 1976b, 1977).

Transections of the adventitious roots show similar anatomical features in all species studied (Fig. 15). The epidermis is typically sloughed in mature roots, and the outer cortex, composed of thick-walled parenchyma cells, forms the outer boundary of the organ. The epidermis, if present, is composed of thick-walled cells filled with tannins. The outer cortical cells also are frequently filled with tannins and may be partially sloughed. The inner cortex, composed of thicker-walled, sclerified parenchyma cells with tannins, typically forms the bulk of the cortex. Previous workers (Schütze, 1906; Sen, 1968) found the position of these two cortical zones reversed, while other investigators (Ogura, 1927, 1972; Lucansky 1976b, 1977, 1982) indicated a similar arrangement for the zones that comprise the cortex in the cyatheoid genera. In *S. senilis* the cortex may be composed of three zones of parenchyma cells, based upon wall thickness. A distinct endodermis composed of a single layer of cells filled with tanniferous substances delimits the stele (Fig. 15). A pericycle (1-2 cells) composed of large, thin-walled, tanniferous parenchyma cells surrounds the vascular tissue. The primary phloem consists of sieve cells and phloem parenchyma, while the primary xylem is composed primarily of scalariform pitted metaxylem and some spiral and reticulate—scalariform protoxylem. The xylem is diarch with exarch maturation (Fig. 15). Vascular parenchyma cells filled with tannins occur between the primary phloem and xylem.

Root traces originate either from a meristele or from the base of leaf traces and pass obliquely through the cortex. Leaf traces arise at successive levels in a leaf gap and proceed to the petiole to form a much-dissected vascular pattern that is similar for all species studied (Lucansky & White, 1974). Both types of traces are identical in cellular composition to the accessory bundles.

Transections of a petiole show similar anatomical characteristics in both *Sphaeropteris* and *Cnemidaria*. A single-layered epidermis composed of small thick-walled, tanniferous cells forms the outer boundary of a petiole. A two-zoned hypodermis occurs beneath the epidermis. The outer zone consists of

large, thick-walled parenchyma cells, whereas the inner zone is typically more extensive and composed of small, sclerified parenchyma cells. Both zones frequently contain tannins, and mucilage-sac cells infrequently occurs in the inner zone in *S. elongata*. Ground tissue, composed of thin-walled parenchyma cells with starch grains and/or tannins, comprises the bulk of a petiole. Large mucilage-sac cells are randomly scattered in this tissue in both genera—either singly or in groups of 2–3 (Figs. 16). Larger groups (4–10) of these idioblasts are infrequently found in *Cnemidaria*. Similar idioblasts were noted in the petioles of the other cyatheoid genera, but are lacking in *Metaxya* (Lucansky 1976b, 1977, 1982). In addition to mucilage-sac cells, small localized areas of sclerified parenchyma cells occasionally occur in the ground tissue of both species of *Cnemidaria*, but are absent in *Sphaeropteris*. These areas arise *de novo*, and are scattered in this tissue. A layer of cubical cells surrounds each area, and also occurs between the ground tissue and inner hypodermal zone in *C. grandis*.

Each petiole strand is surrounded partially or totally by a sheath of thick-walled, sclerified parenchyma cells (infrequently some cells become fibers) (Fig. 16). A layer of cubical cells may occur on both sides of a given sheath in *Cnemidaria*. Cellular composition and arrangement of the stele of each petiole strand is similar to a meristele or accessory bundle of the stem. Tangential cells infrequently occur in the primary phloem in both species of *Cnemidaria*, but are not found in *Sphaeropteris*. The primary xylem is U- or V-shaped, with the protoxylem found in a median position on the concave side of the vascular tissue (Fig. 16). Typically a single, large intercellular space is produced schizolysigenously adaxial to the protoxylem pole in both genera. Previous studies have reported that the protoxylem may partially disintegrate and form a cavity with tyloses (Schutze, 1906; Ogura, 1927), although no cavities were noted in the petioles of other cyatheoid genera (Lucansky 1976b, 1977, 1982).

Based upon the species studied, *Sphaeropteris* and *Cnemidaria* are similar in many anatomical characters, but are significantly different in certain morphological and anatomical features to warrant their generic separation in the Cyatheaceae. Anatomically they are closely related and form a natural group with the other squamate genera in the family, and should not be widely separated in any phyletic scheme proposed for the family.

LITERATURE CITED

- ADAMS, DAVID C. 1977. Ciné analysis of the medullary bundle system in *Cyathea fulva*. Amer. Fern J. 67:73–80.
- BOWER, F. O. 1912. Studies in the phylogeny of the Filicales. II. *Lophosoria*, and its relationship to the Cyatheoideae and other ferns. Ann. Bot. (London) 26:269–323.
- CHRISTENSEN, C. 1938. Filicinae. In *Manual of Pteridology*, ed. F. Verdoorn. The Hague: Martinus Nijhoff.
- GASTONY, G. J. 1973. A revision of the fern genus *Nephelea*. Contr. Gray Herb. 203:81–148.
- . 1974. Spore morphology in the Cyatheaceae. I. The perine and sporangial capacity: general considerations. Amer. J. Bot. 61:672–680.
- . 1981. Spore morphology in the Dicksoniaceae. I. The genera *Cystodium*, *Thyrsopteris*, and *Culcita*. Amer. J. Bot. 68:808–819.
- and R. M. TRYON. 1976. Spore morphology in the Cyatheaceae. II. The genera *Lophosoria*, *Metaxya*, *Sphaeropteris*, *Alsophila*, and *Nephelea*. Amer. J. Bot. 63:738–758.

- GODWIN, H. 1932. Anatomy of the stele of *Cyathea medullaris* Sw. *New Phytol.* 31:254-264.
- HOLTUM, R. E. 1963. Cyatheaceae. In *Flora Malesiana*, Series II, Pteridophyta, Vol. 1 (2):65-176.
- . 1964. The tree ferns of the genus *Cyathea* in Australasia and the Pacific. *Blumea* 12:241-274.
- . 1965. Tree-ferns of the genus *Cyathea* in Asia (excluding Malesia). *Kew Bull.* 19:463-487.
- . 1982. Species of *Cyathea* in the Western Pacific related to *C. multiflora* Sm. and allies in America. *Kew Bull.* 37:383-388.
- and U. SEN. 1961. Morphology and classification of the tree ferns. *Phytomorphology* 11:406-420.
- and P. J. Edwards. 1983. The tree-ferns of Mount Roraima and neighboring areas of the Guayana Highlands with comments on the family Cyatheaceae. *Kew Bull.* 38:155-188.
- JOHANSEN, D. A. 1940. *Plant microtechnique*. New York: McGraw Hill.
- LUCANSKY, T. W. 1974a. Comparative studies of the nodal and vascular anatomy in the neotropical Cyatheaceae. I. *Metaxya* and *Lophosoria*. *Amer. J. Bot.* 61:464-471.
- . 1974b. Comparative studies of the nodal and vascular anatomy in the neotropical Cyatheaceae. II. The squamate genera. *Amer. J. Bot.* 61:472-480.
- . 1976a. The macrotome: a new approach for the sectioning of large plant specimens. *Stain Technol.* 51:199-201.
- . 1976b. Anatomical studies of the neotropical Cyatheaceae. I. *Alsophila* and *Nephelea*. *Amer. Fern J.* 66:93-101.
- . 1977. Anatomical studies of *Cyathea* and *Trichipteris* (Cyatheaceae). *Amer. J. Bot.* 64:253-259.
- . 1982. Anatomical studies of the neotropical Cyatheaceae. II. *Metaxya* and *Lophosoria*. *Amer. Fern J.* 72:19-28.
- and R. A. White. 1974. Comparative studies of the nodal and vascular anatomy in the neotropical Cyatheaceae. III. Nodal and petiole patterns; summary and conclusions. *Amer. J. Bot.* 61:818-828.
- and R. A. WHITE. 1976. Comparative ontogenetic studies in young sporophytes of tree ferns. I. A primitive and an advanced taxon. *Amer. J. Bot.* 63:463-472.
- MAXON, W. R. 1912. The tree ferns of North America. *Smithsonian Inst. Annual Rep.* 1911:473-491.
- MEHRA, P. N. and J. P. SINGH. 1955. Observations of the anatomy of *Alsophila glabra* Hook. *Sci. & Cult.* 21:273.
- OGURA, Y. 1927. Comparative anatomy of the Japanese Cyatheaceae. *J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot.* 1:41-350.
- . 1972. Comparative anatomy of vegetative organs of the pteridophytes. 2nd ed. in K. Linsbauer's *Handbuch der Pflanzenanatomie*. Bd. 7. T. 3. Berlin: Gebrüder Borntraeger.
- SCHÜTZE, W. 1906. Zur physiologischen Anatomie einiger tropischer Farne, besonders der Baumfarne. *Beitr. Wiss. Bot. (Stuttgart)* 5:329-376.
- SEN, U. 1964. Importance of anatomy in the phylogeny of tree ferns and their allies. *Bull. Bot. Soc. Bengal* 18:26-34.
- . 1968. Anatomy of *Culcita macrocarpa*. *Canad. J. Bot.* 46:43-46.
- and D. MITTRA. 1966. The anatomy of *Cystodium*. *Amer. Fern J.* 56:97-101.
- STOLZE, R. G. 1974. A taxonomic revision of the genus *Cnemidaria* (Cyatheaceae). *Fieldiana, Bot.* 37:1-98.
- TRYON, R. M. 1970. The classification of the Cyatheaceae. *Contr. Gray Herb.* 200:1-53.
- and A. F. TRYON. 1982. *Ferns and allied plants*. New York: Springer-Verlag.
- WILLIAMS, S. 1925. Some points on the anatomy of *Dicksonia*. *Proc. Roy. Soc. Edinburgh.* 45:286-296.